Religion, Emotion, and Symbolic Ritual:  
The Evolution of an Adaptive Complex

Candace Alcorta  
Department of Anthropology, U-2176  
University of Connecticut  
Storrs, CT 06269-2176  
calcorta@cox.net

Richard Sosis  
Department of Anthropology  
University of Connecticut  
richard.sosis@uconn.edu  
ph: 860-486-4264  
http://www.anth.uconn.edu/faculty/sosis/

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Abstract

Recent research on the evolution of religion has alternatively viewed religion as a by-product of evolved human mental modules and as a costly signal for social communication. This paper considers religion in relation to five recurrent traits: communal ritual, separation of the sacred and the profane, significance of adolescence in the transmission of religious beliefs, incorporation of counterintuitive concepts, and the presence of supernatural agents. These co-occurring traits are viewed as an adaptive complex that offers clues to the evolution of religion from its non-human ritual roots. We propose that the critical element differentiating religious from non-human ritual is the use of ritual to conditionally associate emotion and abstract symbols. Neurophysiological mechanisms underlying such associations are proposed and the brain plasticity of human adolescence is identified as an “experience expectant” developmental period for ritual conditioning of sacred symbols. We suggest that such symbols evolved to solve an ecological problem by extending communication and coordination of social relations across space and time.

Introduction

The evolution of religion and its possible adaptive function have been the subject of considerable recent research and empirical investigation. Much of this work has been carried out by cognitive scientists who have examined religion in terms of beliefs (Atran 2002; Barrett 2000, Boyer 2001, Bulbulia 2004; Guthrie 1993; Mithen 1996, 1999). This focus on the cognitive aspects of religion has led these researchers, with the notable exception of Bulbulia, to conclude that religion constitutes a by-product of cognitive adaptations selected for “more mundane” survival functions.

Evolutionary anthropologists have also revitalized evolutionary studies of religion over the past two decades (see Sosis and Alcorta 2003). In contrast to the cognitive scientists, however, these anthropologists have tended to focus on religious behaviors rather than beliefs. The primary debate among these researchers has centered on the relative importance of group selection and individual selection on the evolution of religious behavior (Cronk 1994; Rappaport 1994; Sosis 2003a; Sosis and Alcorta 2003; Wilson 2002). Drawing on both ethological studies
and on a rich theoretical legacy beginning with Durkheim (1915[1969]), various evolutionary researchers have proposed that religious behaviors constitute costly signals that contribute to social cohesion (Cronk 1994; Irons 1996 a, b, 2001; Sosis 2003b). This costly signaling theory of religious behavior has subsequently received empirical support from the research of Sosis and colleagues (Sosis 2000; Sosis and Bressler 2003; Sosis and Ruffle 2003). The application of costly signaling theory to religion draws on the foundation laid by Laughlin and McManus (1979) and situates religious ritual within a broader non-human evolutionary continuum by relating it to socially adaptive behaviors. While costly signaling theory has initiated renewed interest in religion by human behavioral ecologists, it has yet to examine how the high levels of cooperation observed within religious communities (e.g., Sosis and Bressler 2003; Sosis and Ruffle 2003) translate into individual fitness benefits.

While not guided by evolutionary analyses, the cumulative finding of a third body of research that has emerged over the past two decades strongly suggests adaptive benefits for religious practitioners. This work has been conducted by sociologists, epidemiologists, psychologists, and physicians, and has explored the health impacts of religion (Hummer et al. 1999; Levin 1994, 1996; Matthews et al. 1998; Murphy et al. 1999). Emergent findings from this research show significant positive associations between religious participation and individual health. These findings, in conjunction with ongoing neurophysiological research on religion (Austin 1998, 2000; McNamara 2001, 2002; Newberg et al. 2001; Saver and Rabin 1997; Winkelman 1986, 2000), suggest proximate mechanisms by which religion impacts individual fitness. They do not, however, address the causal mechanisms from a broader evolutionary perspective.

**Five Features of Religion**

A single definition that encompasses religion’s cross-culturally recurrent features and captures that which differentiates the religious from the secular has yet to be agreed upon. Here we focus on five cross-culturally recurrent features of all religions. These include:

- **Communal participation in costly ritual**;
- **Separation of the sacred and the profane**;
- **Importance of adolescence as the life history phase most appropriate for the transmission of religious beliefs and values**;
Incorporation of counterintuitive concepts in religious belief systems;
Presence of supernatural agents.

The recurrence of these five features of religion in societies as diverse as totemic Arunta hunter-gatherers and Protestant American industrialists suggests that these elements constitute basic traits of religion. The proportionate importance of each element may, and clearly does, vary across religions. We view these co-occurring traits as an adaptive complex that offers clues to the evolution of religion from its non-human ritual roots.

In this paper we will argue that the critical element in the differentiation of religious from non-human ritual was the emergence of emotionally-charged symbols. Following Richerson and Boyd (1998, 1999), we maintain that such symbols solved an ecological problem by extending communication and coordination of social relations across space and time. We propose that symbolic thought had its genesis in the conditioned association of emotions and objects, and we argue that joint participation in ritual was the means by which such conditioning occurred. We view the uniquely human elements of religious ritual, -- including chanting, music and dance, -- as neurophysiologic “primes” for such conditioning, and we propose that the brain plasticity of extended human adolescence constitutes an “experience expectant” developmental period for the emotional valencing of symbolic systems.

Communal Participation in Religious Ritual

The importance of communal participation in ritual as a central feature of religion has been noted by numerous researchers (Bloch 1989; Bourguignon 1973; Durkheim 1915 [1969]; Eliade 1958, 1959; Rappaport 1999; Turner 1967, 1969). The formality, patterning, repetition and rhythm of religious ritual have direct parallels in non-human ritualized display (Laughlin and McManus 1979; Lorenz 1965; Rappaport 1999; Rogers and Kaplan 2000; Smith 1979). In animal species such displays have evolved to serve communication (Dugatkin 1997; Lorenz 1965; Rogers and Kaplan 2000; Rowe 1999). On its most basic level, non-human ritual comprises “a process by which behavior specialized to be informative becomes differentiated from behavior that is informative only incidentally to its other functions” (Smith 1979:54). Ritualized displays incur costs for participants; the more elaborate the display, the costlier the signal in terms of time, energy, and increased somatic insults. Krebs and Dawkins (1984) maintain that such costly signals derive from a manipulative “arms race” between con-specifics.
Zahavi (1975, 1981) has proposed that costly signals evolve as a counter-deception strategy. Empirical research supports his assertion that increasing costliness of signals provides honest information for receiver assessment, since only those fit enough can bear the costs of elaborate displays (Johnstone 2000; Zahavi and Zahavi 1997).

Laboratory studies support the efficacy of ritual as a costly signal. Research has shown that the components of non-human ritualized displays alert and focus attention, enhance memory, and promote associational learning (Rowe 2000). These changes improve the ability of the receiver to assess both the signal and sender “honesty” and neurophysiologically “prime” both the sender and receiver for action (Lewis and Gower 1980; Rogers and Kaplan 2000; Tinbergen 1965). The type of action that results is dependent both upon the receiver’s assessment of the sender and upon the encoded “action releasers” embedded within the ritual display (Lewis and Gower 1980; Lorenz 1965). Ethological studies conducted over the last several decades have clearly demonstrated that animal signals and signal responses show considerable ontogenetic and socio-ecological malleability (Hauser and Konishi 1999; Lewis and Gower 1980; Rogers and Kaplan 2000). Although some species specific signals, such as the pecking response of herring-gull chicks to red dots, constitute relatively fixed, genetically programmed action-response sequences, (Lewis and Gower 1980; Tinbergen 1965), others incorporate individually variant and ontogenetically learned patterns, as seen in the male courtship songs of various bird species (Ball 1999; Marler 1999). Signals of some species, including the aesthetic nest constructions of male bowerbirds (Dissanayake 1995) and the friendship greeting rituals of baboons (Watanabe and Smuts 1999) show considerable malleability and high proportions of learned and novel behaviors. Clearly, a continuum of signal types exists, encompassing a broad range of “fixed” and “learned” elements.

In all species, however, ritual signals elicit neuroendocrine responses that influence social behavior. Such signals simultaneously communicate behavioral intent and convey important information regarding the condition and status of the sender. The intensity of plumage coloration in birds, the pitch of croaking in frogs, and the stotting height of springboks all constitute encoded elements of ritual displays that not only signal sender intent, but also signal information regarding parasite load, size, and agility, respectively (Krebs and Davies 1984; Rogers and Kaplan 2000). They alter behavior as a result of the neurophysiological effects they have on ritual participants (Ball 1999; Dugatkin 1997; Lorenz 1965; Rogers and Kaplan 2002;
Wingfield et al. 1999). Ritualy induced changes in autonomic and neuroendocrine function impact these determinations (Hauser and Konishi 1999; Lewis and Gower 1980; Reichert 2000; Rogers and Kaplan 2000). Ritual signals may initiate, extend, alter, diminish, or truncate social interaction.

Use of Ritual to Invest Abstract Symbols with Emotional Significance.

Religious ritual, like non-human ritualized displays, is demarcated from ordinary behaviors and is composed of the same encoded elements found in non-human ritualized displays (Rappaport 1999). In addition to the formality, patterning, sequencing and repetition of non-human ritual, religious ritual incorporates signals that serve as “action releasers”. The ritualization and sanctification across religions of pan-human social signals of dominance and submission, such as bowing and prostration, have been noted by numerous researchers (Atran 2002; Bloch 1989; Boyer 2001; Leach 1966; Rappaport 1999). As in non-human ritual, such signals serve to elicit innate or ontogenetically derived neurophysiological responses in participants. The transference of such signals from their original contexts to ritual communicates the intent of the sender by evoking the autonomic and neurophysiological state associated with the signal’s ontogenetic origins. The incorporation of food begging displays in bird courtship rituals and presentation of the ano-genital area by subordinate primates to dominants both represent signals that have been emancipated from their original feeding and copulating behaviors and transferred to new contexts of courtship and social hierarchies. In both instances, affiliative responses eliciting approach behaviors are associated with the original function of the signal and the transferred signal intent (Lewis and Gower 1980). Likewise, patterns of muzzle licking in wolf greeting rituals are learned by young pups as part of pack life. Muzzle licking derives from pup feeding behaviors. Muzzle licking in greeting rituals merely transfers the affiliative neurophysiological responses associated with such signals from feeders to leaders. Muzzle licking, thus, constitutes a signal with species-wide neurophysiological salience of ontogenetic origin. Its incorporation as an embedded feature of greeting rituals derives from its pre-existent motivational characteristics (Laughlin and McManus 1979).

While religious ritual incorporates ontogenetically derived signals, such signals are not the primary encoded elements of religious ritual. The fundamental “action releasers” of religious ritual are, instead, abstract symbols devoid of either inherent ontogenetic significance or innate
neurophysiological salience. Unlike the emancipated social signals of non-human ritual, the symbols of religious ritual, by their very nature, have neither pre-existent cognitive nor emotional salience. Words such as “Allah”, geometric designs such as the Star of David, and behaviors represented by such actions as divination and communion, do not, in and of themselves, elicit any innate or ontogenetically derived neurophysiological response. Unlike the signal components of non-human ritualized displays, such abstract symbols do not have intrinsic species significance that primes a particular neurophysiological response. For the non-adherent, religious symbols have no pre-existent cognitive connotations, nor do they elicit any innate emotional response. Unlike the signals of animal ritual, the meaning of religious symbols must be created, both cognitively and emotionally. This important difference between non-human ritual and religious systems requires not only that the abstract symbols of religious ritual be learned; it also requires that the appropriate neurophysiological responses to these symbols be learned, as well. This constitutes the critical difference between human and non-human ritual. While animal ritual elicits behavior through encoded signals, religious ritual elicits behavior to encode symbols. The creation of these symbols provides ritual tools for the shaping of social behaviors across space and time.

Ritual Participation and the Creation of the Sacred

Sosis (2003b) has argued that ritual participation generates belief among performers. He examined the psychological mechanisms underlying this process. Here we extend this argument to explain the interrelationship between emotions, symbols, and the sacred, and describe the neurological underpinnings of how ritual participation impacts belief.

Religious ritual is universally used to define the sacred and to separate it from the profane (Douglas 1969; Durkheim 1915; Eliade 1959; Rappaport 1999). As noted by Rappaport (1999), ritual does not merely identify that which is sacred; it creates the sacred. Holy water is not simply water that has been discovered to be holy, or water that has been rationally demonstrated to have special qualities. It is, rather, water that has been transformed through ritual. For adherents who have participated in sanctifying rituals, the cognitive schema associated with that which has been sanctified differs from that of the profane. For Christians, profane water conjures associations of chemical structure and mundane uses; holy water, however, evokes associations of baptismal ritual and spiritual cleansing. Of greater importance from a behavioral perspective,
the emotional significance of holy and profane water is quite distinct. Not only is it inappropriate to treat holy water as one treats profane water; it is emotionally repugnant. Although the chemical composition of both profane and holy water are exactly the same, a Christian adherent would never drink holy water to slacken thirst. While sacred and profane things are cognitively distinguished by adherents, the critical distinction between the sacred and the profane is the emotional charging associated with sacred things. This distinction in emotional valence is created through participation in religious ritual. Sacred symbols have distinct cognitive schema, but their sanctity derives from their emotional meaning. It is the emotional significance of the sacred that underlies “faith” and directs behavior, and it is through ritual participation that such emotional significance is created. The creation of religious symbols from abstract objects, and the imbuing of these symbols with emotional attributions of “awe”, “purity”, and “danger” (Douglas 1969) are consistent and critical features of religious ritual everywhere (Durkheim 1915; Douglas 1969; Rappaport 1999; Turner 1969). The duration, intensity and developmental timing of the ritual process all contribute to the cognitive and emotional salience subsequently associated with the learned symbols (Glucklich 2002; McCauley 2001; Turner 1967, 1969).

Religious ritual shares a neurophysiological substrate with non-human ritualized displays. Both evoke autonomic and neuroendocrine changes in participants. Such changes in non-human species prime participants for assessment and action in response to ontogenetically encoded signal releasers. The changes elicited through ritual participation in human religious rituals not only prime participants for assessment and action; they also prime participants for the creation of encoded symbolic releasers.

Ritual Participation and the Conditioned Association of Emotions and Abstract Symbols

Participation in religious ritual has been shown to induce changes in autonomic nervous system and EEG activity, as well as in neuroendocrine functioning (Austin 1998, 2000; Brown 2000; Dressler and Bindon 2000; Kasamatsu and Harai 1966; Lex 1979; Newberg et al. 2001; Winkelman 1986, 2000). Accumulating research suggests that emotions derive from autonomic physiological responses (Damasio 1994, 1998; Davidson 1994; Ekman et al. 1983; Levenson 1994, 2002; LeDoux 1996, 2002). Sensory stimuli are first unconsciously processed by the sub-cortical structures of the brain, including the basal ganglia, the amygdala and the hypothalamus.
This system alerts and prepares the body to respond to potential dangers before conscious assessment occurs (Damasio 1994, 1998; Levenson 1994; LeDoux 2002). The central role of the amygdala in this process has particular relevance for the conditioned association of religious symbols. The amygdala, a small, almond-shaped structure tucked beneath the temporal lobe of each hemisphere, is composed of multiple nuclei that play key roles in evaluating the survival significance of stimuli and in generating emotional response. It is particularly important in the elicitation of fear responses, and, in humans, is critical in social judgments of trust (Adolphs 1999, 2002; Adolphs et al. 2002; Dolan 2000; Morris et al. 1998 Oram and Richmond 1999). Animals with lesioned or removed amygdalae lack a fear response, even when placed in highly dangerous situations (LeDoux 1996). Humans suffering from amygdalar dysfunction also exhibit impaired fear response functions (Davidson and Irwin 2002). Additionally, human amygdalar dysfunction negatively impacts facial social judgments (Adolphs 2002; Davidson and Irwin 2002). The amygdala is highly interconnected with numerous sub-cortical nuclei of the brain, and with the pre-frontal cortex. Interconnections of the amygdala with the hypothalamus ensure rapid somatic responses through a cascade of neuroendocrine responses. Interconnections of the amygdala with the pre-frontal cortex are extremely important for social functioning. In the absence of such interconnections, individuals appear to lack the emotional valencing required for effective decision-making (Damasio 1998; LeDoux 1996).

Ongoing research indicates that emotions constitute evolved mechanisms that serve to valence decisions and motivate behaviors (Cardinal et al. 2002; Damasio 1994, 1998; Dehaene and Changeux 2000; Davidson 1994; Frank 1988; Levenson 1994, 2002; Panksepp 1994). They “alter attention, shift certain behaviors upward in response hierarchies, and activate relevant associative networks in memory” (Levenson 1994:123). Emotions “rapidly organize the responses of different biological systems including facial expression, muscular tonus, voice, autonomic nervous system activity, and endocrine activity” (ibid.), and, therefore, constitute potent communication signals between con-specifics (Ekman et al. 1983; 2002). Since emotions are generated from limbic cortices that are out of conscious control, they are difficult to “fake” (Ekman et al. 1983). EEG patterns for simulated and real emotions are not the same, nor are the motor control areas for an emotion related movement sequence and a voluntary act (Damasio 1994, 1998; Ekman and Davidson 1993). As a result, somatic marker signals, including pulse rate, skin conductance, and pupil dilation, as well as facial expressions and body language
generated by emotion, differ from those under voluntary control. Emotions, therefore, provide honest signals of physiological and motivational states. In humans, such signals are processed both consciously and unconsciously by the left and right amygdala, respectively (Adolphs et al. 1998; Davidson and Irwin 2002; Dolan 2000; Morris et al. 1998). Interconnections between the amygdala, the hypothalamus, and the prefrontal cortex allow utilization of the information received from these signals in the regulation of both autonomic and central nervous system responses (Cardinal et al. 2002; Damasio 1994, 1998).

The unique human elements of religious ritual engage both the amygdala and autonomic functions (Lex 1979; Newberg et al. 2001; Winkelman 1986; 2000). Across cultures religious ritual incorporates neuronal firing “drivers” through music, chanting, and dance that alter heart and pulse rate, brain wave patterns, and neuroendocrine levels (Austin 1998, 2000; MacLean et al. 1997; Winkelman 1986, 2000). Human religious ritual shares the stereotypical elements of non-human ritualized displays and further amplifies and intensifies these elements through the incorporation of rhythmic “drivers”. Music, singing and chanting, -- features described by Bloch as “distinguishing marks of ritual” (1989:21), -- differentiate human religious ritual from both secular and non-human ritual. While Bloch derived these features from ethnographies of traditional societies, the recent survey of U.S. Congregations conducted by Chaves et al. (1999) identified these elements as pervasive across modern faiths and denominations, as well. Incorporation of these “rhythmic drivers” in religious ritual has important effects on the neurophysiology of participants, including changes in brain wave patterns, pulse rate, and diastolic blood pressure (Gellhorn and Kiely 1972; Lex 1979; Mandel 1980; Neher 1962; Walter and Walter 1949). Recent clinical research has also demonstrated significant positive correlations between music and immunocompetence, as measured by salivary SIgA (Kuhn 2002). These studies show a graded association of music and immunocompetence, with active participation correlating most highly with immunocompetence, and no music exposure correlating with the least. Ongoing research with ritual participants engaged in meditation and trance show changes in brain wave patterns, heart and pulse rate, and skin conductance, as well as alterations in neuroendocrine levels, including testosterone, growth hormone and cortisol (Austin 1998, 2000; Davidson 1976; Kasamatsu and Hirai 1966; MacLean et al. 1997; Mandel 1980; Newberg et al. 2002; Winkelman 2000). To date, little research has been conducted on the neurophysiological effects of less intense religious participation, such as weekly service attendance. Those studies
that have been undertaken, however, demonstrate effects of participation on autonomic and neurophysiological responses of participants. Both lowered blood pressure (Brown 2000; Dressler and Bindon 2000) and significant and graded inverse correlations between adolescent male testosterone levels and weekly western church attendance (Halpern et al. 1994) have been demonstrated. These findings indicate that participation in even attenuated religious ritual results in changes in autonomic and neurophysiological responses of participants.

Widespread use of hallucinogenic substances in religions cross-culturally may further contribute to such effects through alterations in neurotransmitter levels (Jentsch et al. 2000; Pearson 1990). Additionally, numerous elements of ritual elicit fear, danger and awe (Adolphs 1999; Douglas 1969; Eliade 1959; Turner 1967, 1969). Ritual settings, including caves, caverns and cathedrals, alter sensory perception through unpredictable illumination. Masks, statues, and icons evoke and transform human facial characteristics. These stimuli activate the amygdala, which is involved in both fear responses and facial judgments (Adolphs et al. 1999; Davidson and Irwin 2002). Sleep and food deprivation, as well as painful physical ordeals that affect hypothalamic response, further alter autonomic function and affect both amygdalar and prefrontal processes through extensive hypothalamic-amygdala-prefrontal interconnections (Groenewegen and Uylings, 2000; Rolls 2000). The widespread occurrence of such elements in religious rituals across cultures has two important effects: (1) it increases the firing rate of amygdalar neurons; and, (2) it creates congruent autonomic body states in ritual participants. Each of these effects has important consequences.

Research on temporal lobe syndrome patients has shown that kindling of the amygdala through repeated neuronal firing can result in the conditioned association of arbitrary stimuli with heightened emotional significance (Bear 1979; Bear and Benson 1981; Geschwind 1979; Damasio 1994). The increased religiosity of many temporal lobe epileptics has been attributed to this kindling effect (Bear 1979; Saver and Rabin 1999). Rhythmic environmental stimuli, including both music (Peretz 2001), and rapid, flashing light effects, can trigger the rapid neuronal firing that results in amygdalar kindling (LeDoux 2002). While temporal lobe patients have a low threshold for such firing, experiments have shown that the driving effects of ritual, such as drumming and dancing, alter neuronal firing patterns, as revealed through EEG’s, in non-clinical populations, as well (Lex 1979; Neher 1962; Walter and Walter 1949). A normal distribution of neuronal firing thresholds would account for the range in neurophysiological
responsivity to ritual observed across populations. Increased neuronal firing rates deriving from the rhythmic drivers of drumming, music and dance, coupled with increased activation of the amygdala through fear, pain, and alterations in body state, enhances kindling effects. Research indicates that the basolateral amygdala is responsible for emotional Pavlovian learning through conditioned stimulus-unconditioned stimulus association (Cardinal et al. 2002). Projections from the amygdala to the ventral striatum and the prefrontal cortex (PFC) provide neuronal networks for the conditioned association of religious symbols with emotions (Robbins 2000). The prefrontal cortex plays a critical role in social judgment, impulse control and symbolic thought (Deacon 1997; Dehaene and Changeux 2000; Rolls 2000). The extensive interconnections between the basolateral amygdala and the prefrontal cortex allow the PFC “to gain access to memory and emotional processes” (Groenewegen and Uylings 2002:22). Release of dopamine and noradrenaline in the prefrontal cortex in response to conditioned associations weighs behavioral choices (Feenstra 2000). The emotional weighting of stimuli provided by the interconnections between the PFC and the amygdala is critical for adaptive behavioral choices. Laboratory studies conducted by Schoenbaum et al. (2003) provide neurophysiological evidence that the orbitofrontal cortex of the PFC and the basolateral amygdala “form a functional system involved in the acquisition and use of incentive information to guide goal-directed behavior” (2003:855). This research found that “in addition to becoming linked to representations of outcomes, otherwise neutral cues can acquire motivational significance or value through association with biologically significant events” (ibid:863). In humans, functional imaging studies show orbitofrontal activation in anticipation of rewards and punishments (ibid). Individuals whose prefrontal cortex and amygdalae are intact, but disconnected, perform well on abstract reasoning tasks, but are unable to apply such reasoning to personal decision making in the absence of emotional valencing of choices (Damasio 1994; LeDoux 1996, 2002). The use of religious ritual to activate and kindle amygdalar firing neurologically primes participants for the conditioned association of religious symbols and emotions that subsequently valence individual choices and motivate behavior (Dehaene and Changeux 2000).

The changes in autonomic state and amygdalar activation that result from participation in religious ritual not only contribute to the creation of sacred symbols; they also contribute to experienced empathy among adherents. Recent work by Levenson (2002) indicates that empathy is contingent upon congruent states in autonomic body systems, such as pulse rate, heart
contractility and skin temperature and conductance. The elicitation of congruent autonomic body states in ritual participants through music, dance and chanting allows the creation of communally sacred things through the conditioned association of such states with symbolic words, objects and places. The subsequent use of such symbols to evoke conditionally associated emotions provides a mechanism for eliciting empathetic experiences among adherents across time and space. The creation of emotionally charged symbols through participation in religious ritual provides the neurophysiological scaffolding for empathy, trust, and cooperative group enterprises. Durkheim’s (1915[1969]) assertion that ritual creates social solidarity, and Hayden’s (1987) proposal that religious ritual contributes to inter-group alliances in hominid evolution, recognize this role of religious ritual. Such cognitive scientists as Atran (2002) have also noted religion’s unique ability to unify groups and create moral systems. Empirical research by Sosis (2000), Sosis and Bressler (2003), and Sosis and Ruffle (2003) has demonstrated greater longevity of religious groups, as well as greater commitment among members of religious as compared to secular groups. Sosis and Ruffle (2003) have further demonstrated greater cooperation among religious adherents who communally engage in ritual as compared to those who do not.

In addition to their ability to engender emotions and elicit empathetic responses among adherents, religious symbols further provide rapid assessment cues regarding group membership. As such, they serve as signals of group membership and may well have originated to serve such a function (Dunbar 1999). It is, however, the shared emotional response elicited by such symbols that is of greater long term evolutionary significance. The ability of religious symbols to evoke shared emotional responses allows motivation and coordination of social behaviors across both time and space. The original adaptive value of such symbols may have derived from the shared use of geographically scattered resources and the need to integrate fluid social groups across time and space (Barnard 1999; Henshilwood 2001; McBrearty and Brooks 2000; Watts 1999). The emergence of religious symbols gave conscious form to subconscious emotional and abstract associations. As a result of their ability to impact individual behavior through the conditioned association of sensory, emotional and cognitive stimuli, religious symbols introduced a uniquely human tool for extending social relations and cooperation across time and space.

*Adolescence and Religion*
Adolescent rites of passage comprise one of the most consistent and omnipresent features of religions across cultures (Bettelheim 1962; Brown 1975; Lutkehaus and Roscoe 1995; Paige and Paige 1981; van Gennep 1909[1960]). In some societies, such as the Yamana and Halakwulup of Tierra del Fuego, such rites traditionally consisted of little more than oral transmission of sacred knowledge from elder to youth (Eliade 1958). In other cultures, such as the Ndembu and the Elema, pubertal initiation rites involved “kidnapping” of adolescents, months of sequestered seclusion, and ritual ordeals that include dietary restrictions, sleep deprivation, physical pain and genital mutilation (Eliade 1958; Glucklich 2002; Turner 1969; Paige and Paige 1981; van Gennep 1909[1960]). In modern societies, adolescence also constitutes an important developmental period for religious training (Atran 2002; Elkin 1999; Regnerus et al. 2003). While the intensity and duration of adolescent rites of passage vary from culture to culture, all share a common structure (Turner 1969; van Gennep 1909[1960]), as well as a common emphasis on the evocation of emotion in the teaching of sacred things (Eliade 1958).

The expressed purpose of rites of passage is to initiate particular categories of a society’s adolescents into “the sacred”. Initiates must cognitively learn what things constitute the sacred, but they must also learn the meaning of “the sacred” itself through first-hand experience. This requires the development of new cognitive schemata for previously profane things, whether words, images, or objects, involving the generation of new neuronal associative networks. Most importantly, initiates must simultaneously learn to associate particular emotions with these schemata. The conditioned association of emotion, schema, and symbol, -- the creation of sacred things, -- constitutes the goal of adolescent initiation rites. Adolescent rites of passage seek to instill in initiates new cognitive schema with motivational force. The creation of such schema also creates a cultural community bound in motivation, as well as belief.

Accumulating research suggests that adolescence may constitute a neurophysiologically sensitive developmental period for the learning of abstract concepts and the conditioned association of such concepts with emotions (Kolb et al. 1998; Kwon and Lawson 2000; Plant 2002; Spear 2000). The human brain demonstrates great plasticity during development. Infancy, childhood, adolescence and adulthood are marked by differentiated growth patterns in various brain cortices and nuclei (Casey et al. 2000; Giedd et al. 1999; Keshavan et al. 2002; Kolb and Whishaw 1998; Kolb et al. 1998; Kwon and Lawson 2000; LeDoux 2002; Plant 2002; Romeo et
The differential patterns of brain growth across the life course create sensitive periods for particular types of learning (Greenough 1986). Early childhood language learning constitutes an example of such “experience expectant” learning (Pinker 1997). Adolescence may comprise a second critical period of “experience expectancy” for the learning of emotionally valenced symbolic systems.

While the pre-adolescent brain grows through an increase in cortical gray matter, during adolescence synaptic “pruning” eliminates as much as one-half of the number of cortical synapses per neuron (Spear 2000). Synapse elimination does not occur uniformly throughout the human cortex, however. Frontal and parietal lobes follow a similar developmental trajectory, with increases in gray matter up to a maximum occurring at 12.1 and 11.8 years, respectively, for males and 11.0 and 10.2 years, respectively, for females, followed by a decline, resulting in a net decrease in volume across adolescence. Temporal lobe gray matter has also been found to be nonlinear in growth pattern, with maximum size reached at 16.5 years for males and 16.7 years for females, and slight declines thereafter (Giedd et al. 1999; Sowell et al. 1999). Both frontal and temporal lobe maturation occurs late in adolescent development. This heterochronous adolescent loss of cortical gray matter is accompanied by increases in white matter (Keshavan et al. 2002; Kolb et al. 1998).

White matter density changes reflect increases in axon diameter or myelination. Myelination involves the formation of a lipid sheath around axons and is one of the last stages in neuronal maturation. This sheath facilitates the propagation of electrical signals through the neuron and serves to increase the speed of neuronal transmission (Keshavan et al. 2002; Walker and Bollini 2001). White matter density in both corticospinal and frontotemporal fiber tracts increase during adolescence (Keshavan et al. 2002; Walker and Bollini, 2001). Moreover, limbic structures, including the amygdala and the hippocampus, show an increase in volume, with sex differences in these trends, and ongoing myelination of cells in limbic structures throughout adolescence (Walker and Bollini 2001).

These changes in both gray and white matter during adolescence through synaptic pruning and myelination streamline brain function by eliminating irrelevant interconnections and enhancing those that remain. There is considerable evidence that this ontogenetic sculpting of the brain results from differential activation of specific neurons on the basis of experience in the accommodation of environmental needs (Greenough and Black 1991; Kolb et al. 1998; Kolb and
Whishaw 1998; LeDoux 2002). Work by Kolb et al. (1998) has demonstrated that “experience can alter different parts of neurons differently (and)...changes in synaptic organization are correlated with changes in behavior” (1998:156). As a result, “the environment or activities of the teenager may guide selective synapse elimination during adolescence” (Giedd et al. 1999:863).

The maturation of the prefrontal cortex that occurs during adolescence has important implications for abstract reasoning abilities and symbolic thought. The prefrontal cortex is that brain region “essential for such functions as response inhibition, emotional regulation, planning and organization” (Sowell et al. 1999:860). The interconnectivity of the PFC with nearly all other brain regions uniquely situates this cortical structure in its ability to associate diverse stimuli (Robbins 2000; Rolls 2000). Additionally, the prefrontal cortex receives inputs from and sends outputs to cholinergic cell groups in the basal forebrain and monoaminergic cell groups in the brain stem, including serotonergic, noradrenergic and dopaminergic innervation (Cardinal et al. 2002). This interconnectivity ensures that the PFC is able to influence not only the levels of its own cholinergic and monoaminergic neurotransmission, but also that of other cortical and sub-cortical areas.

Significant changes in neurotransmitter systems occur during adolescence. Receptors for dopamine, serotonin, acetylcholine and GABA are pruned from their pre-adolescent over-production and limbic areas, including the hippocampus, also undergo pruning of excitatory receptors. Hippocampal receptors for endogenous cannabinoids peak during adolescence at higher than adult levels (Spear 2000). Studies by Carlson et al. (2002) demonstrate increased LTP potentiation as a result of endocannabinoid production, suggesting enhanced memory functions during this period. Concurrent with the decline in excitatory neurotransmitter receptors during adolescence, there occurs an increase in inhibitory dopamine input to the prefrontal cortex which peaks during this period (Spear 2000). This increase in PFC dopaminergic systems comprises the mesocortical component of a mesocorticolimbic shift in dopamine dominance occurring during adolescence. This shift in dopamine balance from mesolimbic to mesocortical regions during adolescence impacts reward learning and has significant behavioral implications (Schultz et al. 2002). Dopamine inhibitory input to the prefrontal cortex may be greatest during adolescence, while dopamine activity in the anterior cingulate cortex and other subcortical regions, including the amygdala, may be lowest. Spear
has noted that “these regions form part of the circuitry implicated in drug reward processes, attributing appetitive value or incentive salience to stimuli, translating motivational stimuli into adaptive behaviors, and integrating sensory and motor systems to facilitate flexible approach responses” (2000:443). Structures involved in this circuitry include the amygdala and hippocampus, the anterior cingulate cortex, the ventral striatum, and the prefrontal cortex. While dopamine activity in the anterior cingulate cortex is under inhibitory control of the amygdalar dopamine system, the amygdala is, in turn, tonically inhibited by prefrontal cortex activity. There exists an inverse relationship between metabolic activity in the human amygdala and prefrontal cortex activity (Spear 2000). According to Walker and Bollini, “the enhancement of neuronal connection between the cortex and limbic regions may play a role in the integration of emotional behaviors with cognitive processes” (2001:18) during this time.

The shifting dominance of amygdalar dopamine projections from anterior cingulate cortex to the prefrontal cortex during adolescence impacts both conditioned associations and the intrinsic reward system. In addition to cortical maturation during adolescence, MRI studies have shown differences in the activity of the amygdalar nuclei in adolescents, as compared to adults. Human adolescents exhibit “greater brain activity in the amygdala than in the frontal lobe when engaged in a task requiring the subjects to identify emotional state from facial expressions, while adults conversely exhibited greater activation in frontal lobe than amygdala when engaged in the same task” (Spear 2000:440).

These adolescent changes in brain function have important implications for learning and behavior. Maturation of the prefrontal cortex during adolescence provides the neurophysiological substrate for social cognition, abstract reasoning and symbolic thought (Adolphs 2002a; Deacon 1997; Robbins 2000). The concurrent maturation of the temporal lobe and amygdala are relevant to facial recognition and social judgments (Adolphs et al. 1998). Neuroimaging studies have shown amygdalar activation in the recognition of facial emotional expressions of fear and anger (Adolphs et al. 1999; LeDoux 1996; Morris et al.1999). Additional studies indicate that the amygdala mediates judgment of other people’s social behavior, particularly with regard to approachability and trustworthiness (Adolphs 2003; Cardinal et al. 2002). The shift in the dopaminergic reward system from mesolimbic to mesocortical dominance that occurs during adolescence provides a unique developmental window for the conditioned association of abstract symbols with intensely experienced emotions and for the
integration of this association with social interactions. Heightened adolescent sensitivity to stressors amplifies this process (Spear 2000). The synaptogenesis and neurotransmitter shifts occurring during adolescence intensify the impacts of environmental stimuli experienced during this developmental phase. This is particularly true for the late maturing frontal and temporal cortices, and for such limbic nuclei as the amygdala and the hippocampus.

Adolescent rites of passage bombard initiates with environmental stimuli that engage prefrontal, temporal and limbic functions. The ritual components of these rites optimize stimulus impacts while amplifying the kindling effects of the stimuli through rhythmic drivers, including music, chanting and dance. Intensification of the stimuli, through sleep and food deprivation, fear, and physical ordeals, and drugs can be expected to increase the neurophysiological impacts in terms of memory, reward learning, and emotional charging of stimuli. The “breaking down” of initiates during the liminal phase of adolescent rites of passage engenders a common autonomic state among initiates. The empathy and shared emotional charging experienced in rites of passage valence the cognitive schema associated with sacred things. These experiences literally shape the adolescent brain and provide an organically integrated basis of commitment and belief. As Rappaport noted, through adolescent rites of passage “the abstract is made alive and concrete by the living substance of men and women” (Rappaport 1999:148).

**Incorporation of counterintuitive concepts in religious belief systems**

The incorporation of counterintuitive concepts in religious belief systems is an element common to all religions. Virgin births, undrinkable water, and bleeding statues are all examples of such counterintuitive beliefs. All represent conditions and situations contrary to those which occur in profane existence, and, as cognitive anthropologists have noted, they break inherent rules of basic ontogenetic categories, such as people, animals, and inanimate objects (Atran 2003; Boyer 2001). Why, then, do such concepts consistently recur across religions?

Counterintuitive concepts clearly grab attention. Like the formality of ritual, such concepts mentally alert the message receiver. Precisely because they run counter to profane experience, they engage and focus attention. Counterintuitive concepts also promote memory. Like the sequencing and repetition of ritual, such concepts serve as mnemonic devices that trigger associational neuronal networks. Use of culturally relevant concepts in unexpected and unconventional ways allows quick identification and promotes recall. Research conducted by
Atran and Norenzayan (in press) has empirically verified the mnemonic efficacy of religious counterintuitive concepts. Incorporation of such concepts in religious systems ensures that the message is both heard and remembered.

In addition to their efficacy in arousing attention and increasing memory, counterintuitive concepts allow ready identification of potential free-riders. Since they cannot be derived through logic or experience, they must be learned. And since such learning occurs within the context of ritual participation, knowledge of the concepts implies adherence. The very irrationality of such concepts constitutes an honest signal of commitment to a group who share that belief (Cronk, pers. com). Early Christian belief in the resurrection of Christ constituted a potent signal to both Romans and other Christians. Only individuals knowledgeable about the religious tenets of Roman Catholicism would know about the transmutation of wine to blood, and only those initiated into the faith through the emotional conditioning of those tenets would truly believe that such a transmutation occurs weekly during the sacrament of Communion.

**Presence of Supernatural Agents**

Supernatural agents have been identified as the defining feature of religion by numerous researchers (Atran 2002; Malinowski 1948; Otto 1959; Radin 1957; Tylor 1893). Durkheim was the first to propose that such agents represent the reification of society itself (1915[1969]). His observation that the type of agent represented in a society’s religion reflects the social organization of that society gained support from the work of Wallace (1969) and the cross-cultural research conducted by Swanson (1960). More recently, Guthrie (1993), as well as other cognitive scientists (Atran 2002; Barrett 2000; Boyer 2001; Pinker 1997) have argued that the universal importance of supernatural agents in religions derives from mental modules of human agency that “evolved trip-wired to detect animate agents” (Atran 2002:266). These researchers note religion’s use of supernatural agents as a means to “ensure that moral authority transcends convenient self-interest” (ibid, 268). Some also acknowledge the role played by supernatural agents in “maintaining the cooperative trust of actors and the trustworthiness of communication by sanctifying the actual order of mutual understandings and social relations” (ibid, 278). These researchers stop short of attributing such a function to selection pressures, however, maintaining that “religion has no evolutionary function per se” (ibid, 279).
Yet, when looked at in terms of ritual continuum, the emergence of religion from non-human ritual would appear to be directly related to the problem of communicating and maintaining social relations across time and space. While ritual signals serve to directly order and maintain such relations within the immediate here and now through direct impacts on the neurophysiology of ritual participants, they lack the ability to extend these impacts over time or distance since they require direct and immediate conspecific interaction. Religious ritual solves this problem by creating and recreating symbolic releasers that elicit neurophysiological responses in adherents across time and space. The conditioned association of such releasers with cognitive schemata reflective of the social order, as that represented by supernatural agents, constitutes a fundamental component of this process. Such schemata simultaneously give form to the abstraction of social relations while divorcing that form from the particularities of a specific time and place. They must be both motivational and flexible, and, in the absence of writing, they must also be highly memorable. Supernatural agents provide highly memorable and emotionally girded generic symbols that function to maintain social relations across time and space.

Conclusion: Evolutionary Significance of Religion

Most contemporary evolutionary studies of religion begin with cognitive analyses, focusing on the beliefs rather than the behaviors of religious systems. Yet, from both a cross-cultural and cross-species perspective, it is ritual that lies at the heart of all religions, and it is participation in ritual that both creates adherents and results in empirically demonstrated effects on individual fitness. Ritual in non-human species functions to communicate social information and to coordinate social behaviors through the use of species signals evolved to elicit neurophysiological responses. Religious ritual, too, functions to communicate and coordinate social behaviors and does so through the elicitation of neurophysiological responses. In contrast to non-human ritual, however, religious ritual employs symbols to extend ritual’s ability to communicate and coordinate social behaviors across time and space.

The imbuing of religious symbols with emotional meaning through ritual participation is fundamental to religion’s efficacy. This is achieved through the conditioned association of culturally designated things, -- whether beliefs, words, places, or objects, -- with ritually generated cognitive schemata and emotional responses. The uniquely human use of music, art, and dance as constant components of religious ritual are integral to this process. Also integral to
this process is the unique period of extended human adolescence and the brain plasticity it incorporates.

Through the conditioned association of religious objects with emotional significance, religious ritual provides a mechanism for neurophysiologically regulating social relations. It extends the spatial and temporal boundaries of social relations and, in so doing, creates an abstract social order that exists outside of and beyond realized conspecific interactions. The ability of religious ritual to create associational networks linking sensory, social and emotional schemata lies at the heart of symbolic thought. Thus, rather than a by-product of third order cognition, religious ritual promulgates such cognition through the symbolization of abstractions. For early hominid groups inhabiting large ranges of patchy resource distribution, the ability to predict and coordinate group behaviors beyond the immediacy of face-to-face contact would have been vital to survival. The evolution of religious symbols from the signals of animal ritual solved this ecological problem, and, in so doing, altered the course of human cognition and culture.

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